Review



Translational photobiology: towards dynamic lighting in indoor horticulture

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Crop productivity depends on the ability of plants to thrive across different growth environments. In nature, light conditions fluctuate due to diurnal and seasonal changes in direction, duration, intensity, and spectrum. Laboratory studies, predominantly conducted with arabidopsis (*Arabidopsis thaliana*), have provided valuable insights into the metabolic and regulatory strategies that plants employ to cope with varying light intensities. However, there has been less focus on how horticultural crops tolerate dynamically changing light conditions during the photoperiod. In this review we connect insights from photobiology in model plants to the application of dynamic lighting in indoor horticulture. We explore how model species respond to fluctuating light intensities and discuss how this knowledge could be translated for new lighting solutions in controlled environment agriculture.

From basic plant photobiology to horticultural lighting

Photosynthetic primary production is remarkably responsive to the direction, duration, intensity, and spectral guality of light. In the field, neighboring plants, wind-induced canopy movements, and climatic and seasonal alterations give rise to a fluctuating light (see Glossary) environment that can significantly affect the efficacy of primary production, unless continuous photosynthetic adjustments are made [1,2]. In basic research, fluctuating light refers to a light environment in which periods of low light and high light alternate during the photoperiod. The light-induced adjustments reflect shifts in light conditions over seconds, minutes, hours, and days. Photobiological responses occur at the molecular, cellular, and whole-plant levels, ranging from transient photosynthetic rearrangements to light acclimation involving changes in gene expression, metabolism, and growth [3,4]. A meta-analysis of 500 experiments with 760 plant species demonstrated that plant chemistry, physiology, anatomy, morphology, growth, and reproduction are all responsive to the daily light integral (DLI; µmol photons m⁻² day⁻¹) [5]. Laboratory studies on fluctuating light have, however, centered on the model plant arabidopsis. In many cases, research outcomes have been discussed in terms of plant productivity in the field [2,6,7]. Much less is known about how vegetable crop species respond to changing light conditions and whether dynamic lighting strategies could be applied in indoor horticultural production. Here, dynamic lighting refers to indoor cultivation conditions in which the intensity of artificial lighting alternates during the cultivation period.

This review examines how the current body of knowledge on plant performance under fluctuating light could be applied in designing dynamic lighting for indoor cultivation (Figure 1). Light-emitting diode (LED)-based technologies could allow tailoring of cost-effective, dynamic lighting strategies to reduce problems arising from fluctuating electricity spot prices. Dimming and brightening of luminaire intensity, mirroring fluctuations in electricity price, could considerably lower the production costs since the light intensity output of LEDs is directly proportional to the usage of electrical current [8]. From a photobiological perspective, well-optimized changes in light intensities could induce acclimation processes that enhance the accumulation of antioxidants, phenolic

Highlights

Plant light acclimation enables crop productivity in different environments in which the direction, duration, intensity, and spectrum of light varies due to diurnal or seasonal changes.

Laboratory studies on model plants have uncovered fundamental regulatory mechanisms which enable coordinated acclimation responses to varying light intensities.

A thorough understanding of plant light acclimation is a prerequisite for the development of dynamic lighting strategies in which the light intensity is intentionally alternated during the cultivation period in controlled environment agriculture.

Light can considerably affect the resilience, color, flavor, and nutritional value of vegetables. In a well-optimized dynamic lighting strategy, the intensity of light changes according to the price of electricity, allowing cost-effective growth without compromising the nutritional or sensory quality of horticultural crops.

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Trends in Plant Science

Figure 1. Bridging plant photobiology to dynamic lighting in indoor horticulture. Automated LED-based lighting solutions could forward cost-effective indoor cultivation of vegetable crops. In dynamic lighting strategies, the intensity of light is alternated during the photoperiod. The potential energy saving arises from usage of dimmable LEDs, whose energy consumption is directly proportional to the light intensity, which can be adjusted mirroring the electricity price. Basic photobiological research on model plants, notably *Arabidopsis thaliana*, and translational research on crop species are needed to uncover how plants respond to changing light conditions, with the goal to attain cultivars best suited for cultivation under dynamic lighting. Implementation of dynamic lighting strategies necessitates interdisciplinary investigation of crop productivity, nutritional value, sensory properties, and consumer acceptance. Abbreviation: LED, light-emitting diode. Figure created with biorender.com.

compounds, and species-specific phytochemicals, which affect the resilience, color, flavor, and nutritional value of vegetables [9,10]. For a discussion on how light spectral composition affects the quality of plants in controlled environment agriculture, please refer to recent reviews [11–13].

Photosynthetic light reactions feature overlapping photoprotective systems

Light is the driver for photosynthetic electron transfer and carbon assimilation [14]. In linear photosynthetic electron transfer, electrons flow from Photosystem II (PSI), plastoquinone, cytochrome b6f complex (Cytbf), plastocyanin, and photosystem I (PSI) to ferredoxin and NADP⁺, generating reducing power in the form of NADPH in chloroplast stroma. The thylakoid electron transfer reactions are coupled with proton translocation into the thylakoid lumen, and the consequent formation of a proton motive force across the thylakoid membrane drives the production of ATP by the ATP synthase. From PSI, a share of electrons is diverted to thioredoxins, which link photosynthetic electron transfer with regulation of various metabolic processes. Thioredoxinmediated reduction of regulatory thiol groups controls a variety of metabolic enzymes, which consume NADPH and ATP for carbon fixation, starch biosynthesis, and other biosynthetic processes in chloroplasts [15–18].

Excess excitation energy may cause accumulation of electrons in the thylakoid electron transfer chain, especially when accumulation of reducing equivalents in the form of ferredoxin and

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NADPH exceeds their consumption in carbon metabolism. This increases the likelihood of electron transfer to molecular oxygen, thus promoting formation of reactive oxygen species (ROS) [19]. Light-induced imbalances in the electron transfer of PSII may promote oxidative damage and photoinhibition of the PSII complex [20–24]. High-light-exposed plants therefore accumulate various antioxidants, notably ascorbic acid, carotenoids, tocopherols, and phenolic compounds to manage light-induced oxidative metabolism and signaling [25–28]. In horticultural settings, light-induced biosynthesis of antioxidants and photoprotective pigments can improve the nutritional guality of vegetables and herbs [11,29,30].

Acidification of the thylakoid lumen is central in various photoprotective systems within the thylakoid membrane [31] (Figure 2). A key mechanism is pH-dependent dissipation of excess excitation energy as heat at the light-harvesting complex of PSII (LHCII), which can be measured as changes in qE, the most rapidly reversible component of non-photochemical quenching of chlorophyll fluorescence (NPQ) [20,32,33]. Activators of qE include the PsbS protein, also called NPQ4, which mediates structural rearrangements required for NPQ activation in the PSII antenna [34–36]. Another key player activated by luminal protonation is violaxanthin de-epoxidase (VDE), also known as NPQ1, which generates the photoprotective pigment zeaxanthin that enhances NPQ [37]. Apart from proton translocation coupled with photosynthetic electron transfer, light-regulated ion transport across the thylakoid

Glossary

Dynamic lighting: an emerging indoor cultivation practice in which the intensity of artificial lighting is intentionally changed during the cultivation period. For example, the light intensity for growth may be adjusted according to the price of electricity.

Fluctuating light: a light environment in which periods of low light and high light alternate during the photoperiod. Fluctuating light may arise from diurnal and seasonal changes in natural conditions or may be introduced artificially in laboratory experiments. Light acclimation: light-induced molecular, physiological, and developmental responses that allow plants to cope with varying light conditions.



Figure 2. Overlapping short-term regulation of photosynthetic light reactions. Extensive basic research has uncovered overlapping regulatory systems that enable photosynthetic adjustments and generation of stromal reducing equivalents and ATP under changing light conditions. Acidification of thylakoid lumen activates non-photochemical quenching of excess excitation energy (NPQ). Trans-thylakoid ion homeostasis is maintained by linear and cyclic electron flow, ATP synthesis, and ion transport across the thylakoid membrane. Cyclic electron flow involves distinct PGR5 and NDH-dependent pathways. Lateral movement of photosynthetic pigment-protein complexes, together with biochemical adjustments in the composition and post-translational regulation of photosynthetic machinery provide yet another dynamic level of regulation within the thylakoid membrane. Abbreviations: Cytb6f, cytochrome b6f complex; Fd, ferredoxin; FNR, ferredoxin-NADPH oxidoreductase; FTR, ferredoxin-thioredoxin reductase; KEA3, thylakoid K*-exchange antiporter; NDH, NADH dehydrogenase-like complex; NPQ, non-photochemical quenching; PC, plastocyanin; PGR5, PROTON GRADIENT REGULATION 5; PQ, plastoquinone; PSI, photosystem I; PSII, photosystem II, STN7, protein kinase STATE TRANSITION 8; TRX, thioredoxin. Figure created with biorender.com.





membrane affects the acidification of the thylakoid lumen and thereby shapes the dynamics of NPQ [6,38].

Pathways of cyclic electron transfer recycle electrons from PSI to plastoquinone and affect the generation of the proton gradient across the thylakoid membrane, while shuttling electrons away from the reach of stromal redox components. Cyclic electron flow therefore affects NPQ and the ratio in which NADPH and ATP are produced [39,40]. Cyclic electron transfer involves PROTON GRADIENT REGULATION 5 (PGR5) and PGR5-LIKE PHOTOSYNTHETIC PHENOTYPE1 (PGRL1) proteins, as well as the chloroplast NADH dehydrogenase-like complex (NDH), both routes being vital in maintaining photosynthesis upon environmental challenges [41–45]. Yet another process connected with lumen acidification is photosynthetic control, whereby downregulation of electron transfer through the cytochrome b6f complex protects PSI from light-induced damage [46]. At the level of light harvesting, state transitions balance the transfer of excitation energy between PSII and PSI [47–49]. This balancing act involves reversible phosphorylation and relocation of LHCII, regulated by counteracting activities of the protein kinase STATE TRANSITION7 (STN7) and the protein phosphatase PPH1 [50–52]. Additionally, the large pigment–protein megacomplexes undergo dynamic light-dependent reorganization to optimize photosynthetic reactions [53].

The complexity of the overlapping systems requires comprehensive understanding of the mechanisms at play. For in-depth reviews on thylakoid proton motive force, NPQ, cyclic electron flow, state transitions, and possibilities to tackle their impacts by chlorophyll fluorescence measurements, the reader is referred to recent reviews [3,6,23,31,54–56].

Insights from studies on fast photosynthetic adjustments under fluctuating light Fluctuating light conditions were first generated in small-scale rotating experimental platforms [50,57,58], but more recently large-scale phenotyping platforms with adjustable LED light intensity and duration settings have allowed simulation of fluctuating light in a more controllable manner [17,59]. Fluctuating light experiments were often designed to cause light stress with periods of low and high light alternating on a time scale of minutes [55,58,60-62]. Morales et al. [3] pointed to reduced biomass accumulation under fluctuating light, as opposed to growth under constant light intensity. Moreover, Vialet-Chabrand et al. [63] found that arabidopsis grown under fluctuating light developed thinner leaves compared with plants grown under moderate constant light. The available information concerning growth penalties should be carefully considered when optimizing growth conditions for commercial production, to avoid light stress to an extent that could impede productivity [64]. Recently, Kaiser et al. [65] provided evidence that dynamic lighting can support crop growth, as the marketable fresh weights of basil (Ocimum basilicum), pak choi (Brassica rapa subsp. chinensis), rucola (Diplotaxis tenuifolia), and spinach (Spinacia oleracea) were unaffected by growth under hourly alterations in light intensities, when compared with growth under constant light conditions with equal DLI.

Studies on arabidopsis mutants have enabled the discovery of components involved in photosynthetic adjustments under fluctuating light [54,61,66–68] (Figure 2). The photoprotective function of PGR5 has been extensively studied [39,43,60,61]. Suorsa *et al.* [60] grew wildtype and *pgr5* mutant plants under 120 µmol photons $m^{-2} s^{-1}$ for 5 weeks, and then shifted to fluctuating light, where low light intensity of 50 µmol photons $m^{-2} s^{-1}$. After 9 days, biophysical characterization of wild-type plants revealed that the 1-min high light pulse induced significant regulatory adjustments, including enhanced NPQ, oxidation of PSI, and high proton motive force across the thylakoid membrane [60]. By contrast, all of these adjustments



were absent in *pgr5*, reflecting the central function of PGR5 in triggering the pH-dependent downregulation of the b6f complex to safeguard PSI from photodamage [39,60]. Germinating *pgr5* mutants were particularly sensitive and died under fluctuating light, demonstrating that the severity of the *pgr5* mutant phenotype depended on plant developmental stage [58,60].

Kühlheim *et al.* [57] reported that arabidopsis *npq1* and *npq4* mutants, deficient in the key components of qE, were severely affected in seed production under fluctuating light. The *npq* mutants showed no drastic growth defects in rosette size, whether subjected to fluctuating light in a laboratory experiment or to natural conditions in the field [57,58,67]. Hence, exposure to fluctuating light may have different effects in different plant tissues and developmental stages. In the context of crop selection for indoor farming, a dynamic light condition harmful to fruit crops might still be suitable for leafy vegetables.

Slow relaxation of NPQ upon shift from high to low light could prolong the dissipation of excitation energy and limit growth by wasting light energy that could otherwise drive photosynthesis [2,69-71]. To overcome this limitation, De Souza et al. [71] accelerated the violaxanthin xanthophyll cycle by combining overexpression of arabidopsis violaxanthin de-epoxidase (V), PsbS (P), and zeaxanthin epoxidase (Z) in transgenic VPZ soybean (Glycine max cv. 'Maverick'). This resulted in increased photosynthetic efficiency and seed yield, while seed protein and oil contents remained unaltered under naturally fluctuating light in field conditions. Transgenic VPZ potato (Solanum tuberosum L. cv. 'Solara'), by contrast, showed decreased tuber yield when grown under fluctuating light (50 μ mol photons m⁻²s⁻¹ for 5 min and 500 μ mol photons m⁻²s⁻¹ for 1 min) in a greenhouse [72]. Arabidopsis VPZ-overexpressors grown under similar fluctuating light conditions also failed to increase biomass accumulation [62]. These contrasting findings suggest that photobiological responses can depend on both the plant species and its growth environment. In indoor cultivation settings, unnecessary dissipation of light energy as heat can be considered a waste of energy. This speaks for the importance to optimize the frequency of light fluctuations, as every change in light intensity could cause a transient limitation in photosynthetic capacity (Figure 1).

Adjustments in photosynthetic performance depend on the frequency, duration, and intensity of fluctuating light [38,63,73,74]. Yin and Johnson [74] tested how fully expanded arabidopsis rosettes respond to transition from a steady growth light of 100 µmol photons m⁻² s⁻¹ to various fluctuating light conditions. These conditions entailed alternating light intensities of 100 and either 475 or 810 µmol photons m⁻² s⁻¹, occurring at intervals of 15 min, 1 h or 3 h during the photoperiod. Transferring the plants to fluctuating light resulted in increased oxygen evolution capacity of PSII [74]. Whether this was due to light fluctuation, or increased DLI as a consequence of the high light illumination, remains to be established, but the extent of photosynthetic adjustments clearly depended on the combination of duration and intensity of high light under the fluctuating light conditions [74]. Alter et al. [73] applied more drastic conditions and grew plants under 50 µmol photons m⁻² s⁻¹ and tested the effects of 20 s high light peaks at 650 or 1250 μ mol photons m⁻² s⁻¹ every 6 or 12 min. These differences in light intensities activated NPQ and ROS scavenging systems, while the efficiency of PSII and leaf growth declined [73]. These two examples illustrate that responses to short, stressful high-light pulses can differ from acclimation responses to longer high-light treatments. Moreover, fluctuating light may increase DLI and therefore have a positive impact on photosynthesis, and different fluctuating light conditions can trigger different physiological responses in different genotypes [65,75–82]. However, studies with both short and long episodes of high light have demonstrated upregulation of antioxidant systems under fluctuating light [17,60,73].



Matthews *et al.* [83] focused on physiological adjustments in arabidopsis and compared stomatal function under fluctuating light regimes, which differed with respect to the scheduled pattern of illumination but summed up to a similar DLI. Examination of gas exchange demonstrated different stomatal kinetics depending on the intensity and pattern of illumination, with differences in the magnitude and speed of the stomatal response [83]. Again, the frequency of light fluctuations is relevant in the context of indoor cultivation, since slow opening of stomata upon shift to high light could transiently restrict the availability of carbon dioxide for photosynthesis [84,85].

Just like high-light stress, low light can limit plant productivity if photosynthetic carbon metabolism becomes limited by diminished production of reducing equivalents or ATP. The molecular mechanisms behind light use efficiency during low light phases of dynamic lighting should therefore be examined. For example, transient relocation of chloroplasts could be critical in facilitating light harvesting under the low-light phase of fluctuating light [86–90]. Combinations of high and low light episodes should be tested on different crop genotypes to unleash the full potential of indoor cultivation in terms of crop yield and light-induced metabolic changes.

Gene expression and metabolic interactions promote tolerance to fluctuating light

Light acclimation is governed by complex transcriptional networks that activate in response to fluctuating or sustained changes in light levels. Schneider *et al.* [91] first grew arabidopsis for 4–5 weeks under constant growth light at 75 µmol photons $m^{-2} s^{-1}$, and then shifted to fluctuating light with 20 s pulses at 1000 µmol photons $m^{-2} s^{-1}$ every 5 min for 3 days. Adding the high light pulses to the constant light background induced notable changes in transcripts related to photoprotection, photosynthesis, photorespiration, and components related to pigments, prenylquinone, and vitamin metabolism [91]. The gene expression changes differed between young and mature leaves, and between samples harvested in the morning and evening. A follow-up study further compared the transcript data with matching proteomic datasets, highlighting protein-specific responses and the importance of post-transcriptional regulation in light acclimation [92]. These findings suggested that acclimation to fluctuating light involves regulatory interactions related to photopical processes, leaf developmental stage, and the time of day [91,92].

In another experimental setting, a daily 4 h exposure to a sixfold increase above growth light for 5 days resulted in the acclimation of photosynthetic electron transport and enhanced carbon assimilation [93]. Central to this process were the transcription factors HY5 and BBX32, which integrate light signals and coordinate the expression of downstream genes [93]. Overexpression of BBX32 perturbed the expression of genes related to light harvesting, electron transport, and carbon fixation, which was consistent with its negative impact on acclimation [93]. Collectively, the reprogramming of gene expression related to photosynthesis, pigment metabolism, ROS responses, and photoprotection is highly conditioned by the light environment. To gain wider insight, Balcke *et al.* [28] extended to multiomics analysis and observed concerted responses in gene expression, redox proteomes, and metabolite contents in arabidopsis leaves upon shift to constant high light. Likewise, integrating gene expression and metabolomics data from crop species under dynamic lighting could be informative to map the regulatory pathways underlying acclimation to a given lighting condition.

Light-induced metabolic interactions can be hard to predict, as recently demonstrated by analysis of arabidopsis photorespiratory mutants under fluctuating and constant light [78]. Photorespiratory mutants displayed impaired growth under constant light conditions, but growth under fluctuating light ameliorated the growth retardation phenotypes [78]. As an



outcome of in-depth analysis of growth, photosynthesis and metabolic flux, the authors concluded that reduced rates of photosynthesis, together with re-routing of metabolic flux, could explain the somewhat unexpected findings. The plasticity of plant metabolic networks may buffer plant growth and metabolism against photobiological perturbations. Analysis of crop performance under fluctuating light should therefore be extended to in-depth metabolomic examination. Crop cultivars should be screened for favorable metabolic responses, such as desirable accumulation of sugars and starch, which contribute to the sweetness and cooking characteristics of plant-based food. In some cultivars, high light could enhance the accumulation of specialized metabolites with undesired sensory characteristics, such as bitterness or astringency, which could decrease consumer acceptance and should therefore be avoided [10].

Until now, basic research has revealed that plant developmental stage, tissue specificity, genotype, and the applied lighting, along with other environmental conditions, are critical determinants of plant photobiological responses. While it has been proposed that applying data from laboratory experiments to field conditions may require a reality check [82], studies conducted under fluctuating light in controlled growth cabinets can be highly relevant in advancing applications in indoor cultivation.

Extending basic photobiological research to crops under dynamic lighting

Indoor farming is energy-intensive, largely due to its reliance on artificial lighting, which can cover up to 70–80% of electricity costs in commercial production [8,65,94]. Modern indoor farming with dimmable LEDs and automated control systems optimizing their electricity consumption, mirroring the fluctuating electricity spot prices, could enhance year-round availability of fresh, locally cultivated vegetables [94]. Introducing new lighting technologies will, however, necessitate interdisciplinary studies assessing how lighting affects the productivity, visual appearance, texture, mouth feel, flavor, nutritional value, shelf life and consumer acceptance, aspects that are now coming into focus [12,65] (Figure 1).

Advancements in large-scale phenotyping platforms with adjustable LED panels and imaging systems, alongside omics profiling and advanced data analysis, can significantly forward horticultural research [82]. These technologies enable validation of dynamic lighting regimes for crop species, thus facilitating the translation of fundamental photobiological insights into practical applications. The increasing availability of genomic information, coupled with the abundance of germplasm serving as genetic resources for crop genomic diversity, provides possibilities for testing hypotheses arising from studies conducted on model plants. Comparing different cultivars, landraces and wild accessions under dynamic lighting will unveil photobiological responses in crop species in indoor settings. With increasing knowledge of molecular mechanisms behind plant photoprotection, gene candidates for breeding improved crop productivity have been proposed [6]. Combining high-throughput phenotyping with advanced statistical analysis can enable identification of candidate genes behind traits of interest [95,96]. This will advance the selection of crop genotypes suitable for crossing in traditional breeding programs and identify candidate enzymes for manipulation by biotechnological breeding for indoor cultivation (Figure 1).

Leafy vegetables as experimental models in dynamic lighting research

Productivity, in terms of leaf biomass is an important attribute that should be maintained, or even increased, under dynamic lighting. Leafy vegetables and herbs have rapid growth cycles and represent good models for studies on dynamic lighting [65]. Lettuce (*Lactuca sativa*) is a well-annotated model with different cultivars available for plant physiology research. As a proof of concept for applicability of dynamic lighting on lettuce, Bochenek *et al.* [97], showed that differential delivery of the DLI, with a 6 h high-light period during the early or late hours of the photoperiod, did



not cause growth defects in biomass accumulation of four-week-old lettuce cv. 'Galiano' plants. Likewise, low-high light fluctuations in photosynthetic photon flux density every 15 min over 6 weeks did not negatively affect growth and chlorophyll content in 'Little Gem' and 'Green Salad Bowl' lettuce [98]. In these studies, the fluctuations in light conditions were rather mild compared to light conditions used in basic research on arabidopsis [58,60,91]. While promising results in terms of biomass yield have been reported [65,97,98], dynamic lighting has not been comprehensively tested with different crop species and cultivars, and potential photobiological effects on chemical composition and food quality remain largely unknown [12,29,65,97–99].

Leafy crops within the family Brassicaceae, such as kale (*Brassica oleracea* cv. *acephala*) and watercress (*Nasturtium officinale*) represent attractive options for indoor farming due to their rapid growth and high content of nutritionally beneficial specialized metabolites. Particularly characteristic of plant species of the family Brassicaceae is the presence of glucosinolates, which are S- and N-containing specialized metabolites that contribute to the pungent flavor of brassica crops. Ishihara *et al.* [30] showed that growth of kale cv. 'Black Magic' under constant highlight conditions at 800 µmol photons m⁻² s⁻¹ at 26°C promoted the accumulation of aliphatic glucosinolates and anthocyanins, both of which are nutritionally beneficial due to their antioxidant activities. Even though the study was conducted under constant high light, these findings encourage larger-scale studies with a wide selection of cultivars to enable tailoring cultivar-specific dynamic lighting regimes, aiming to lower the production costs while maintaining crop quality.

Concluding remarks

Combining crop genetic diversity with advanced lighting technologies – including optimized spectral, intensity, and photoperiodic settings of lighting – is key to optimizing cultivation conditions to a crop of interest. However, both agrotechnological and photobiological questions regarding optimized usage of dynamic lighting in cost-effective controlled-environment agriculture remain to be resolved. Further, studies on the impacts of light intensity changes on crop quality should be extended to sensory analysis and survey of consumer acceptance. This understanding is crucial for increasing the production and consumption of plant-based food (see Outstanding questions).

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Declaration of interests

No interests are declared.

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Outstanding questions

What kind of agrotechnological solutions will enable automated and profitable dynamic lighting?

To what extent can different crops and cultivars tolerate dynamic lighting without declining quality or yield?

How does usage of dynamic lighting affect the nutritional quality, texture, mouth feel, and other sensory characteristics, and consumer acceptance of vegetables?

Which molecular mechanisms of plant light acclimation are relevant when developing dynamic lighting in indoor horticulture? Can these mechanisms be genetically modified to improve productivity in controlled environment agriculture?



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